

MODIFICATION OF SEA ANEMONE BEHAVIOR BY SYMBIOTIC ZOOXANTHELLAE: EXPANSION AND CONTRACTION

VICKI BUCHSBAUM PEARSE¹

Hopkins Marine Station, Pacific Grove, California 93950

No specialized photoreceptors have been identified in sea anemones, but it has been demonstrated repeatedly that at least some anemones react to visible light (*e.g.*, Hargitt, 1907; Parker, 1917; Cotte, 1921, 1922; Batham and Pantin, 1950; North and Pantin, 1958; di Milia and Geppetti, 1964; Clark and Kimeldorf, 1970; Ottaway, 1973). And the most frequently reported reaction is contraction. Contraction is not a specific response to light, however. It is provoked by almost any strong stimulus that might be considered unfavorable: vigorous mechanical or electrical stimulation, a variety of chemicals, exposure to air, extremes of temperature, osmotic shock, X-radiation, etc. (*e.g.*, Torrey, 1904; Piéron, 1906; Fleure and Walton, 1907; Parker, 1917; Hall and Pantin, 1937; di Milia and Geppetti, 1964; Kimeldorf and Fortner, 1971).

A large number of anemones expand in twilight or darkness and contract in daylight. Parker (1917) reviews reports of a dozen genera, some with several species that have been observed to behave in this way; and 3 or 4 genera are reported to be indifferent to light. In contrast, I have found only a few reports of anemones that regularly expand by day. Bohn (1907, 1908a, 1910) affirms that specimens of *Actinia equina* from certain habitats expand in daylight and contract at night, while those from other habitats show exactly opposite behavior. Di Milia and Geppetti (1964) found that this species consistently expands in darkness and contracts in light. *Anemonia sulcata*, an anemone that harbors symbiotic zooxanthellae, is reported to expand in the light and contract in the dark (Gosse, 1860; Bohn, 1906; Smith, 1939). Finally, Gee (1913) observed regular expansion in light and contraction in darkness by specimens of *Anthopleura elegantissima* with zooxanthellae. There are similar reports for polyps of several gorgonians with zooxanthellae (Wainwright, 1967; Chapman and Theodor, 1969).

Various authors have propounded diverse views of the factors which influence expansion and contraction in sea anemones. The difficulties encountered may be illustrated by comparing Bohn's (1908b) listing of 36 environmental factors which affect expansion and contraction with Batham and Pantin's (1950) finding that expansion and contraction continue in the apparent absence of any environmental stimuli. I have made no attempt to resolve the hypothetical effects of all these factors. However, as part of a more extensive study on the symbiosis of *Anthopleura elegantissima* with zooxanthellae (Buchsbaum, 1968; Pearse, 1974), I have observed differences in the expansion of specimens with and without the endosymbiotic algae and have tried to evaluate the possibility that this behavior is related to the symbiosis.

¹ Present address: Division of Natural Sciences, University of California, Santa Cruz, California 95064.

METHODS

Specimens of the sea anemone *Anthopleura elegantissima* (Brandt, 1835) with and without zooxanthellae were collected from rocky intertidal areas in central California, and zooxanthellae were eliminated from some specimens in the laboratory by exposure to elevated temperature, as detailed previously (Buchsbaum, 1968; Pearse, 1974).

Recording of expansion and contraction was simplified by the fact that the large majority of sea anemones were usually either fully expanded or fully contracted under experimental conditions. Arbitrary decisions were necessary only occasionally. The anemones were not fed.

Anemones were observed in the laboratory both in standing sea water and in running sea water. Light was provided by a bank of fluorescent tubes operated automatically on an alternating cycle (12 hours light: 12 hours dark). Observations during the dark period were by dim white or green (540 nm Klett filter) incandescent light; the period of exposure to these dim light sources was never more than a few seconds, and the anemones were not observed to react to them.

Standing sea water

Single animals were placed and allowed to attach in open glass jars 5 cm in diameter, containing about 100 ml sea water, in a temperature-controlled room at 12° C. The light intensity was about 450 foot-candles, as measured with a Photovolt 200 photometer, approximating midafternoon light readings of the intertidal habitat where the anemones with zooxanthellae were collected. Records of expansion and contraction of individual anemones were kept. Oxygen determinations by the Winkler method (Strickland and Parsons, 1965) were made using single animals in similar, sealed jars, under the same conditions of temperature and light (see Figure 1).

Running sea water

Groups of 30 animals each were placed and allowed to attach in open plastic boxes (20 × 28 cm, 10 cm deep), and the total number of animals expanded or contracted was recorded at intervals (see Table I, Figures 2 and 3). A continuous flow of sea water at 14° C ± 1° was maintained through the boxes. The light intensity was approximately 250 foot-candles, chosen as intermediate in the habitat range of the anemones in this experiment.

RESULTS AND OBSERVATIONS

Anemones in standing sea water

In observations over 8 days, the anemones without zooxanthellae, collected from a shaded intertidal habitat (midafternoon light intensity about 2 foot-candles), did not expand or contract in response to a daily cycle of light and darkness. At the beginning of the experiment, when supplied with fresh sea water, they stayed mostly expanded in light and dark. Left for the rest of the time in stagnant sea

water, they contracted and remained so. In contrast, the anemones with zooxanthellae showed a very regular pattern of expansion in light and contraction in darkness throughout the experiment. The animals usually expanded within about 10 minutes after the light was turned on. Two anemones from which all zooxanthellae were eliminated in the laboratory were also observed; these animals behaved as did the anemones naturally occurring without zooxanthellae, remaining contracted throughout most of the experiment.

Anemones without zooxanthellae, even those that had been contracted for several days, expanded within minutes after the sea water was renewed or thoroughly stirred, or after air or oxygen was bubbled through. Bubbling nitrogen through the sea water did not stimulate expansion of contracted anemones.

The oxygen content of the sea water was measured in similar but sealed jars containing single anemones with and without zooxanthellae under the same conditions of light and temperature as in the behavior experiments. The oxygen data for experiments of 12 hours in light or dark (Figure 1) show that in the light, the oxygen content of the sea water increased substantially in jars containing sea anemones with zooxanthellae. Addition of light and dark values for each individual anemone with zooxanthellae gives mixed positive and negative results;

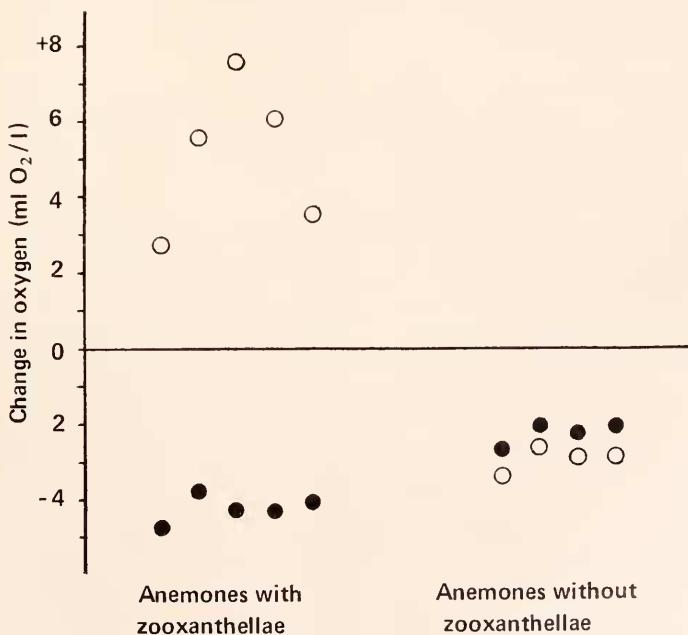


FIGURE 1. Changes in oxygen content of sea water surrounding 5 anemones with zooxanthellae and 4 anemones without zooxanthellae, in light (open circles) and darkness (solid circles), after 12 hours. The oxygen content of the sea water at the start of each experiment averaged 5.66 ml O_2/l of sea water and decreased a maximum of 0.15 ml O_2/l in control vessels containing no anemones. Values in the figure were corrected for changes in control vessels.

TABLE I

Expansion of anemones in light and dark in running sea water. Light intensities of the habitats from which the anemones were collected were measured under clear skies in midafternoon. The values for the percentage of anemones expanded are means and standard deviations of data for 10 days.

	Light intensity of habitat (foot-candles)	% Expanded	
		Light	Dark
Clone from a deeply shaded habitat Group 1, without zooxanthellae	2	100	95.7 ± 6.0
Clone from a habitat spanning a range of light intensities			
Group 2, without zooxanthellae	2	100	91.2 ± 7.6
Group 3, with few zooxanthellae	40	100	49.4 ± 13.0
Group 4, with zooxanthellae	210	99.6 ± 1.1	27.5 ± 9.9
Clone from an open habitat			
Group 5, with zooxanthellae	450	99.4 ± 1.5	23.8 ± 10.2
Group 6, without zooxanthellae (all eliminated in the laboratory)	450	98.9 ± 2.0	38.9 ± 11.8

but experiments run continuously for 24 hours (12 hours light + 12 hours dark) consistently yielded negative oxygen values, suggesting microbial growth.

Anemones in running sea water

Expansion and contraction data from observations of anemones in running sea water are presented in Table I. Virtually all of the anemones, both with and without zooxanthellae, expanded in the light. Anemones without zooxanthellae, collected from shaded intertidal habitats (Groups 1 and 2), remained expanded in the dark also. In contrast, the large majority of anemones with abundant zooxanthellae (Groups 4 and 5) contracted in the dark, just as they did in standing sea water experiments. The anemones from an intermediate habitat with dim light, containing few zooxanthellae (Group 3), showed intermediate behavior; in the dark, about half remained expanded and half contracted.

The anemones that had previously harbored zooxanthellae, but had been caused to eliminate the algae in the laboratory (Group 6), did not remain continuously expanded as did the anemones naturally occurring without zooxanthellae. Rather, like the anemones with zooxanthellae, the majority of anemones that had lost their zooxanthellae expanded in the light and contracted in the dark.

The time course of expansion and contraction is illustrated in Figures 2 and 3. A majority of the anemones responded within 10 minutes after the lights were turned on or off, and by 20–30 minutes, all had usually responded. However, during the 12 hours of continuous light or darkness that followed, some variability in behavior often appeared, especially in the dark. This variability is evident in the observations summarized in Table I, which were always made toward the

middle or end of the light and dark periods. This procedure was chosen in order to record a sustained level of response rather than the more dramatic 0% or 100% expansion that was usually observed immediately after a change in light phase. If the lights were turned on or off in the middle of a 12-hour dark or light period, both the time course and percentage of anemones responding were the same as when the lights went on or off after the usual 12-hour interval.

Field observations

Field observations were limited to anemones with zooxanthellae found in tide-pools at low water, since animals exposed to air by the receding tide almost invariably contract, and no anemones without zooxanthellae were found in suitable pools. In pools viewed at dawn, all of the anemones were contracted. As the daylight gradually increased, they suddenly began to expand, until all were fully expanded after 20–30 minutes. The time course of dawn expansion in the field under a gradually increasing light intensity was thus the same as the time course in the laboratory, where the lights were turned on suddenly (Figure 2). On slightly overcast days, the anemones remained fully expanded. However, on clear days, the animals contracted in midday sunlight. At such times, the distribution of expanded and contracted anemones in the pools corresponded exactly to the pattern of shadow and sunlight, respectively. No temperature differences in the sea

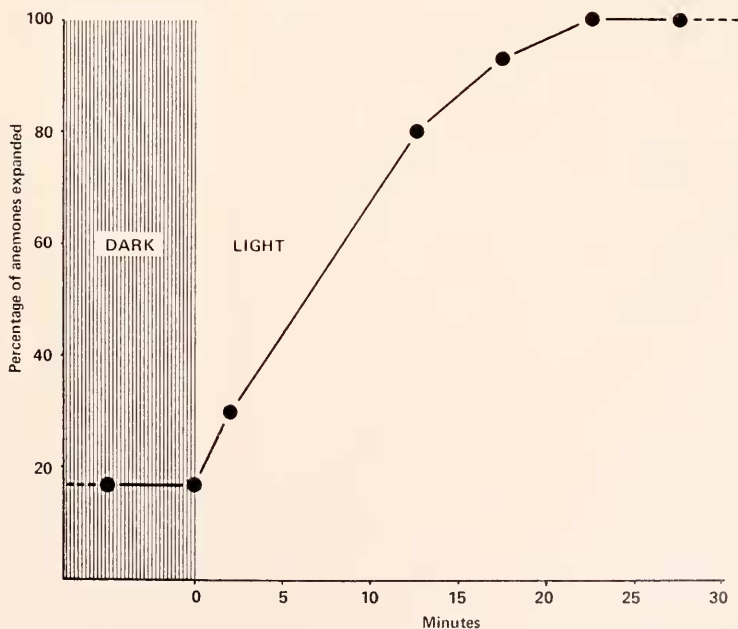


FIGURE 2. Time course of expansion by sea anemones in running sea water. The data presented are from a group of anemones with zooxanthellae, but the time course was the same for anemones that had lost their zooxanthellae.

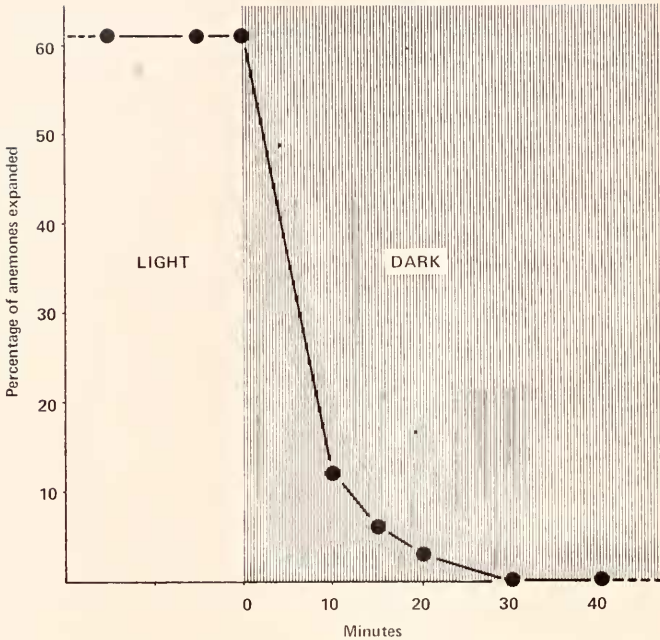


FIGURE 3. Time course of contraction by sea anemones in running sea water. The data presented are from a group of anemones with zooxanthellae, but the time course was the same for anemones that had lost their zooxanthellae.

water could be found to account for the distribution; however, internal temperatures of the anemones were not determined.

Observations on anemones in outdoor tables and tanks with running sea water supplemented intertidal observations. Anemones with zooxanthellae expanded in diffuse daylight but contracted in direct sunlight; they contracted on moonless or cloudy nights, but expanded fully in bright moonlight. Anemones from which zooxanthellae had been eliminated followed the same pattern. The behavior of anemones without zooxanthellae originating from dark habitats was erratic.

DISCUSSION

Observations on the sea anemone *Anthopleura elegantissima*, in both standing and running sea water, have shown differences in the behavior of individuals with and without zooxanthellae. Anemones without zooxanthellae, originating from dark habitats, do not regularly expand or contract with changes in light. In contrast, anemones with zooxanthellae expand in moderate light and contract in intense light or darkness, with striking uniformity. I have found also that individuals without zooxanthellae do not display phototaxis, while those with zooxanthellae show positive or negative phototaxis depending on the light intensity

(Pearse, 1974). The pattern of expansion and contraction in this sea anemone is thus similar to that of its phototactic behavior in that both are modified by symbiosis with zooxanthellae. In both kinds of behavior, anemones without zooxanthellae appear basically indifferent to light while anemones with zooxanthellae engage in active, light-related responses.

Behavior in both standing and running sea water suggests that the anemones without zooxanthellae generally expand in well-oxygenated sea water and contract when oxygen levels fall. A direct response to oxygen is further implicated by the rapid expansion of contracted individuals in stagnant sea water after renewal or stirring of the sea water or gassing with air or oxygen, and by the lack of expansion after gassing with nitrogen, which provided similar mechanical stimulation.

Anemones with zooxanthellae may also be responding to changes in oxygen concentration, rather than directly to light. The oxygen data in Figure 1 indicate that in the light photosynthesis by zooxanthellae met the respiratory requirements of both algae and anemone and raised the oxygen content of the sea water, as has been found in other cnidarians with zooxanthellae (*e.g.*, Yonge, Yonge, and Nicholls, 1932; Smith, 1939; Kanwisher and Wainwright, 1967; Roffman, 1968; Chapman and Theodor, 1969). In the dark, with the zooxanthellae no longer producing oxygen, its concentration fell. However, most of the anemones were contracted after only 10 minutes of darkness (see Figure 3), and it seems unlikely that oxygen content was much reduced in that short time. In running sea water, where anemones without zooxanthellae hardly ever contracted, it is especially difficult to explain contraction of anemones with zooxanthellae by a hypothesis of oxygen deprivation, unless they require much more oxygen. However, they may respond simply to a sudden reduction of available oxygen, regardless of absolute concentration. In the dark, the lower oxygen values recorded for anemones with zooxanthellae (Figure 1) probably reflect only the larger size of these particular individuals, compared with those lacking zooxanthellae; the respiratory burden added by the zooxanthellae was not determined. Use of specific photosynthetic inhibitors (see, *e.g.*, Vandermeulen, Davis, and Muscatine, 1972) or determination of the action spectrum of the response (see, *e.g.*, Clark and Kimeldorf, 1970) may help to establish whether expansion and contraction are direct responses to light or to some consequence of photosynthesis.

In standing sea water, accumulation of metabolic by-products excreted by the anemones might also lead to contraction. There is evidence that other cnidarians excrete less phosphorus (Yonge and Nicholls, 1931a, 1931b; Smith, 1939; Yamazato, 1966) and less nitrogen (Kawaguti, 1953; Muscatine, in press) when zooxanthellae are present, and that at least some respiratory carbon dioxide is fixed by zooxanthellae (Pearse, 1970). In the light, individuals of *A. elegantissima* with zooxanthellae excrete into the sea water only about half as much ammonia as do those lacking zooxanthellae, nitrogen being recycled between host and algal cells (L. Muscatine and C. D'Elia, University of California, Los Angeles, personal communication), and it seems likely that excretion of phosphorus compounds and carbon dioxide is also reduced. Accumulation of excretory products might also influence contraction indirectly through enhancement of microbial

growth in the jars of standing sea water. Comparison of oxygen data from 12- and 24-hour experiments suggests that microbial respiration was considerable; and I observed that the sea water in the jars containing anemones without zooxanthellae became cloudy after several days, while that in the jars containing anemones with zooxanthellae remained clear.

However, if a direct response to change in available oxygen or any other consequence of photosynthesis by zooxanthellae were the only factor regulating expansion and contraction, the anemones from which zooxanthellae had been eliminated would be expected to behave exactly like anemones naturally occurring without zooxanthellae. This was indeed observed in standing sea water, where oxygen depletion or accumulation of excretory products could rapidly have become a determining factor. But in running sea water, like anemones with zooxanthellae, individuals that had lost their zooxanthellae expanded in light and contracted in darkness. This suggests the possibility that the anemones' behavior was conditioned by their previous symbiosis. Also suggestive of conditioning were the apparent changes in the behavior of anemones naturally occurring without zooxanthellae, which took place after prolonged exposure, not to endosymbiotic algae, but to seaweeds in intertidal pools and diatoms in laboratory vessels (see Buchsbaum, 1968 for details). I did not carry out any experiments specifically designed to test for evidence of conditioned behavior in these animals. However, in view of the number of recent suggestions that cnidarians are capable of simple forms of learning (see review by Rushforth, 1973), the expansion and contraction of these sea anemones seems a promising experimental system to investigate further.

How contracting in the dark might be of special selective advantage to a sea anemone with zooxanthellae is obscure. Decreased oxygen consumption has been reported in contracted sea anemones (Piéron, 1908; Shoup, 1932; Smith, 1939), including *Anthopleura elegantissima* (see Buchsbaum, 1968 for details). An intertidal anemone such as *A. elegantissima*, which often produces dense populations in isolated tidepools, may be subjected to low oxygen conditions during low tides, especially at night. Since oxygen consumption by at least some anemones (Sassaman and Mangum, 1972), including *A. elegantissima* (J. J. Childress, University of California, Santa Barbara, personal communication), is proportional to the oxygen concentration of the surrounding sea water, it might be to the anemone's advantage to reduce its rate of oxygen consumption by contracting when the oxygen concentration first begins to drop. However, these anemones appear to survive low oxygen conditions for long periods, and contraction may simply conserve energy.

Possible selective advantages of the anemones' behavior in light are easier to defend. Under moderate light intensities, expansion exposes the abundant zooxanthellae in the tentacles and oral disk to maximum illumination and thus presumably favors maximum photosynthesis. Oxygen data from gorgonians suggest that less light reaches the zooxanthellae in retracted polyps than in extended ones, due to shading by ectoderm and spicules, especially in strongly pigmented species (Kanwisher and Wainwright, 1967; Chapman and Theodor, 1969). In intense light, however, maximum exposure of zooxanthellae may instead reduce photo-

synthesis. Roffman (1968) suggests that in scleractinian corals with zooxanthellae, midday decreases in photosynthesis are related to extended exposure to high light intensity. Thus, contraction by *A. elegantissima* in bright sunlight may serve a significant function in shielding the zooxanthellae in the endoderm beneath the heavily green-pigmented ectoderm of the column of the animal. Ectodermal pigments are produced by these anemones under the influence of bright light, and poorly pigmented individuals from partially shaded habitats suffer substantial reduction in number of zooxanthellae and total chlorophyll when suddenly exposed to increased light intensities (Buchsbaum, 1968). The sea anemone *Actiniogeton sesere*, which occurs in shallow waters of Hawaiian reef flats and harbors zooxanthellae, produces extremely heavy concentrations of a similar green pigment in the tentacles and oral disk; these anemones remain expanded in full sunlight (Buchsbaum, 1968).

Development of pigmentation (Buchsbaum, 1968) and phototaxis (Pearse, 1974) may represent two mechanisms by which the sea anemone *Anthopleura elegantissima* favorably regulates the quantity of light to which its symbiotic zooxanthellae are exposed. These are both relatively slow responses and probably serve principally to permit the animal to select and adapt to habitats in a wide range of light intensities. Expansion and contraction provide a more rapid and flexible means for regulating the light reaching the zooxanthellae as light levels rise and fall from minute to minute throughout the day.

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SUMMARY

The pattern of expansion and contraction by the sea anemone *Anthopleura elegantissima* differs in individuals with or without endosymbiotic zooxanthellae. Anemones without zooxanthellae, found in dark habitats, do not regularly expand or contract under changes in light. Anemones with zooxanthellae expand in moderate light and contract in intense light or in darkness, with striking uniformity.

However, this behavior does not always depend directly on the presence of zooxanthellae. Anemones that have previously had endosymbiotic zooxanthellae subsequently expand and contract with changes in light in the absence of these algae. Thus, conditioned responses may be involved.

It is suggested that expansion and contraction of the anemones may play an important role in favorably regulating the amount of light to which their zooxanthellae are exposed.

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